near Whakapapa Cottage, 3700 ft., 9. i. 1922 (*Miss S. Hudson*).

Although this differs in general appearance from most species of *Macromastix*, and rather strongly suggests a species of *Holorusia*, the fleshy ovipositor and the absence of a spur in cell *M* show that it has no close connection with *H. novaræ* and allied species. On the other hand, it shows considerable affinity with the species of the *viridis* group of *Macromastix*, and seems to have a near ally in *M. angusticosta*, Alex., which has no nasus, femora with black tips, etc.

LXXIII.—*On the Larva, Pupa, and Systematic Position of* Orphnephila testacea, *Macq.* (*Diptera Nematocera*).

By L. G. Saunders, M.Sc. (McGill), 1851 Research Student*.

[Plates VII. & VIII.]

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History.

The adults of *Orphnephila* have long been known in Europe, from Lappland and Norway to Italy; one species, *O. testacea*, occurs sparingly in the United States, and very recently a number of species have been discovered in New Zealand and Tasmania. Prior to the discovery of the early stages, a special family, Orphnephilidæ, was erected to accommodate this embarrassing genus, which would not conform to the specifications of any family among the Nematocera; Macquart, Meigen, and Kieffer agreed in placing it between the Mycetophilids and the Cecidomyids.

In 1909 Thienemann found the larvæ and pupæ of *O. testacea* living in small streams and brooks, where the water runs very thinly over smooth rocks. When appealed to, Kieffer at once pronounced that this was a Chironomid, and the group was made the first subfamily of the Chironomidæ, with the Ceratopogoninæ second. This information was published by Thienemann (1909) with a brief description of the early stages, accompanied by a discussion of the other insect-larvæ which live under similar conditions.

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Bezzi (1913) is still of the opinion that *Orphnephila* represents a distinct family, related on one side to the Blepharoceridæ and on the other to the Psychodidæ-Culicidæ and the Chironomidæ, but not to be joined to them, being of earlier origin than any of these groups. He based his opinion on a critical study of the adults and his own interpretation of the larva apparently from Thienemann's description, since he furnishes no additional morphological characters.

In 1914 Thienemann sent material of the immature stages to Dr. D. Keilin at the Laboratoire d'Évolution des Êtres Organisés, Paris. Unfortunately, pressure of work prevented Dr. Keilin from studying the characteristics of the larva, and he has now very generously permitted me the use of the original material.

HABITS OF LARVA AND PUPA.

For the benefit of those who may wish to search for this interesting species, the details of the life-history as far as known are here reproduced from Theinemann's paper.

The eggs and oviposition are unknown.

In habitat the larvæ are very specialised, being found only in small brooks and streams where clear clean water flows very thinly (about 1 mm. deep) over rocks, so that the back of the larva is always exposed above the surface. The food of the larva consists of vegetable detritus and diatomes. When searching for food a creeping motion is employed, using the prothoracic pseudopod and mandibles after the manner of Chironomids. Faster progression is achieved by a special method which Theinemann states from his very wide experience to be different from that of any other dipterous larva ; the fore part of the body is bent sideways in an inverted U drawing the posterior end of the body as far forward as possible, and then straightened out again suddenly, the venter always remaining in contact with the substratum. A consecutive series of such motions performed rapidly enables the larva to proceed at a good pace.

Pupation and emergence occur from summer to late autumn (November). The pupæ lie on the bottom between stones and aquatic plants, and are not seen as frequently as the larvæ.

DESCRIPTION OF LARVA.

The following description of the colour and appearance of the living larva is translated from Thienemann's paper, since only preserved material is available for this study :—

"Length of full-grown larva 14 mm., width about 1 mm. Number of segments, head + 12 segments. General appearance that of a Chironomid larva. Colour: venter white. Dorsum and pleuræ whitish green, marbled with dark grey-green. In the young larvæ the light tones predominate; those about to pupate are much darker. Segments 1 and 2 are darker than the rest; the light marbling first developes in segment 3. Chætæ black. Head light reddish brown, bent strongly downwards."

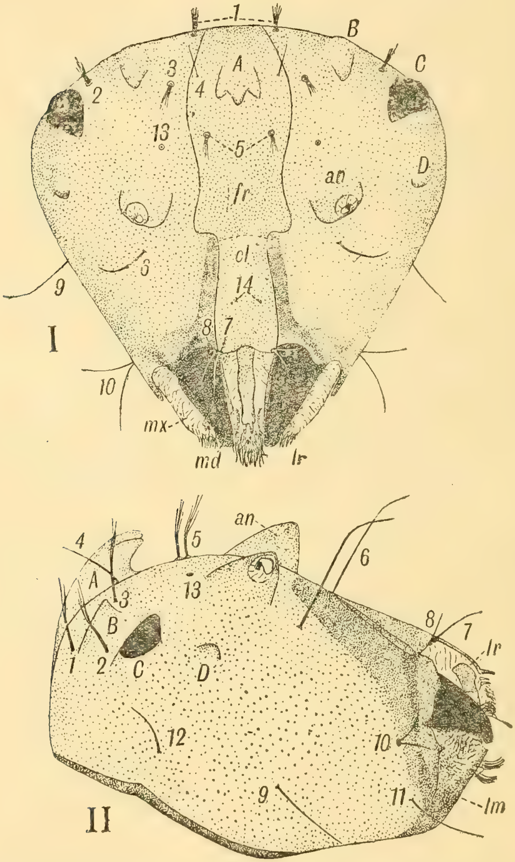
Head.—Complete; well chitinised; bent ventrally at a sharp angle, resembling in this respect *Forcipomyia* and *Atrichopogon*, Ceratopogonines (Malloch, 1915). A unique condition exists in the presence of three pairs of cone-like protuberances and a median, unpaired, trilobed protuberance of the chitinous capsule of the head (text-fig. 1, I. & II., *A, B, C, D*). These all point in an antero-ventral direction. The protuberance *C* contains the pigment of the *eye-spot*, and its surface is slightly modified to form a rudimentary lens. The *antennæ* consist each of a sensory ring accompanied by a group of three minute finger-like processes situated in a membranous area on the top of a cylindrical, obliquely truncated protuberance (Pl. VII. fig. 5, and *an*, text-fig. 1) on either side of the frons, in practically the same position as in *Forcypomyia*.

Chætotaxy: twelve pairs of chætæ occur upon the head, arbitrarily numbered 1–12, and two pairs of sensory pits, 13 and 14. Chætæ numbers 1, 2, 3, and 5 are stout and strong at the base, but at a point rather less than half their length they flatten and split into a number of hairs, usually four. The other chætæ of the head are simple; at 10, two hairs arise from a common opening in the chitin.

The *frontal* and *clypeal sutures* are distinct throughout their length, and, though no actual transverse suture divides the frons from the clypeus, the latter separates very readily during dissection at the point indicated by a dotted line in text-fig. 1, I., and Pl. VIII. fig. 11. From this point, just outside the clypeal suture, a very strong inner thickening of the wall of the head extends forward to fuse with the thickened ring surrounding the mouth-parts, and to send off a strong inner projection which serves as fulcrum for the mandible.

Mouth-parts.—*Labrum* (Pl. VIII. figs. 11, 12): the form of the labrum is quite distinct from that of any other Nematocerous larva. A narrow band of chitin passes along the dorsum from the anterior margin of the clypeus, and terminates in two tapering conical processes (*cp*) ; the end of the labrum is membranous, bearing several sensory processes (*snp*) and a lateral fringe of short hairs (*fh*). From the end of the median dorsal strip of chitin, the labrum, as seen from the side, curves gradually downward

Fig. 1.



I. Head of larva, front view, ×70. II. The same, lateral view, ×70. *A–D*, protuberances of head; 1–14, chætæ and sensory pits; *an*, antenna; *cl*, clypeus; *fr*, frons; *lm*, labium; *lr*, labrum; *md*, mandible; *mx*, maxilla.

until it recurves to form the roof of the mouth ; the ventral side of this anterior portion consists of a single curved chitinous plate (*vp*), above which on the anterior surface are two divided sensory processes. The remainder of the ventral surface leading back to the mouth is membranous, and exhibits at one point a setaceous area. The sides of the labrum are membranous except for one chitinous plate (*lp*), at the anterior end of which are two comb-like groups of long curving hairs (*ch*). Premandibular structures of any kind are completely lacking.

The *mandibles* (*md*, Pl. VIII. figs. 14 & 15) are roughly triangular, strongly chitinised, somewhat flattened laterally, and coarsely denticulate. A large stiff brush of setæ occurs on the inner ventral margin, directed into the mouth; three slender sensory hairs are situated on the dorsal outer surface.

The *maxillæ* (*mx*. Pl. VIII. figs. 14, 15) are fairly well developed. A basal chitinous ring or band encircles the maxilla almost completely; the remainder of the walls are membranous. Two groups of sensory papillæ (*spp*) occur upon the upper portion, and two dense rows of serrated setæ (*ss*) are situated on the anterior surface. The maxillæ are attached by their dorsal margin to the mandibles much more strongly than to the head, and for this reason the two organs have been figured together.

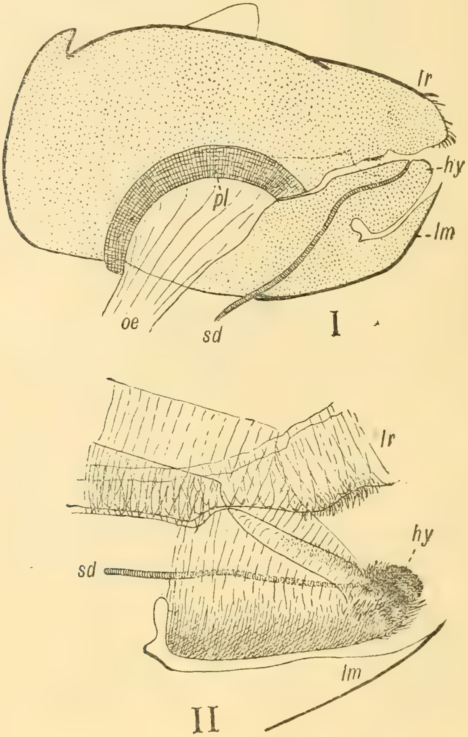
The *labium* (Pl. VIII. fig. 13): the terminology of the ventral and inner mouth-parts is so confused and uncertain that I prefer to retain this name for the chitinous underlip when it occurs as simply and distinctly as in the present case, and "hypopharynx" for the inner portion. The labium is a nearly triangular plate of thick chitin with a row of blunt terminal teeth; it is directed upwards from the ventral side of the head at a sharp angle (text-fig. 2), and is fixed and immovable. A membrane from its inner surface proceeds back into the head, and returns as the hypopharynx.

The *hypopharynx* (text-fig. 2) is a fleshy organ lying just above the labrum; its anterior portion is bilobed, with curious serrated chitinous thickenings and membranous areas bearing sensory papillæ. The *salivary duct* opens just behind this anterior portion on the dorsal surface. The remainder of the surface of the organ forms the floor of the mouth-cavity, and is continuous with the pharynx.

The *pharynx* is strengthened above on either side by a pair of large, sickle-shaped, striated lamellæ (text-fig. 2, I., *pl*). The members of each pair are closely appressed, the outer being connected with the hypopharynx, and the inner with the labrum. A similar condition exists in the larvæ of Ptychopteridæ, Rhyphidæ (Keilin, 1912), and Culicidæ (Johannsen, 1903), but the two pairs are always more or less widely separated in the middle, remaining joined at their extremities.

Body.—The body of the larva consists of three thoracic and eight abdominal segments, the eighth being divided into two apparent segments, as is so often the case in the Nematocerous Diptera (de Meijere, 1919). Each segment bears a peculiar dorsal "saddle" of reticulated chitin; histological preparations of fresh material are necessary to reveal the true nature of this structure.

Fig. 2.



I. Graphic saggital section of head to show relation of internal mouthparts, ×70. II. Hypopharynx, lateral view, ×200. *hy*, hypopharynx; *lm*, labium; *lr*, labrum; *œ*, œsophagus; *pl*, pharyngeal lamellæ; *sd*, salivary duct.

The prothoracic segment bears an antero-ventral pseudopod in the form of an undivided retractile evagination of the wall of the venter, surmounted by a row of long, closely-set hooks (Pl. VII. fig. 2). Several rows of hooks of varying sizes beneath the anus function as a posterior pseudopod (Pl. VII. fig. 10).

The larva is amphipneustic: a pair of *spiracles* occur on the upper sides of the prothorax at the lower margin of the "saddle"; these are in the form of a short black cylinder (Pl. VII. fig. 7) with an extended lip studded with minute points, the ends of very fine canals. Functional spiracles also occur upon the dorsum of the eighth abdominal segment (*usp*, Pl. VII. fig. 9) on the anterior half between two large, conical, fleshy protuberances. The two tracheæ unite just below the cuticle and share a common elliptical spiracle. The structure of these spiracles will be discussed in detail by Dr. Keilin in a forthcoming paper on respiration in insects.

The extremity of the abdomen bears two pairs of slender, digitate, *anal blood-gills* above the anus (*ag*, Pl. VII. fig. 10).

Chætotaxy: the macrochætæ have a tendency to go in pairs and to be split at the end into two, three, or four. On the first seven abdominal segments there are two pairs of chætæ at the ventral margin of the dorsal "saddle," the anterior pair simple, the posterior split (Pl. VII. fig. 1). The three thoracic and eighth abdominal segments show a slight modification of this arrangement. The latter bears a dorsal split pair just above the anus, and behind the posterior spiracle a pair of processes more like slender chitinous tubercles surmounted by four chætæ (Pl. VII. fig. 10).

Numerous microchætæ are present on the sides and venter, but these do not exhibit any regular arrangement. The ventro-lateral thoracic groups representing the rudimentary sense-organs of the absent legs (*sl*, Pl. VII. fig. 1) consist of two pairs of hairs each, the ventral pair long and slender, the dorsal very short (Pl. VII. fig. 4).

DESCRIPTION OF PUPA.

The pupa (Pl. VII. fig. 3) presents a curious angular appearance occasioned by the prominent dorsal and lateral shields or plates with which the first seven abdominal segments are furnished. The thorax is corrugated into numerous ridges and hollows. The *prothoracic horns* are large, approximately vase-shaped, flattened laterally, with a row of spiracular papillæ (de Meijere, 1902) encircling the truncated extremity (Pl. VII. fig. 6).

The most important characteristic of the pupa is that it is *peripneustic*, having spiracles (Pl. VII. fig. 8) on all the abdominal segments but the first and last. Thienemann overlooked these, but figured a structure on the metathorax which he thought might be a spiracle; my two specimens, being rather poorly preserved, do not show this structure, but no doubt spiracles could be found here in fresh material.

Systematic Position.

It will be seen from the foregoing description that the resemblance of *Orphnephila* larvæ to the Chironomids is merely superficial, being based on the long slender body with anterior and posterior pseudopods—characters which may readily be acquired by convergence. The more fundamental characters, such as the mouth-parts and respiratory apparatus, show no such relation. The fact that the larva is amphipneustic and the pupa peripneustic is alone sufficient to exclude *Orphnephila* from the Chironomidæ, for, despite Brauer's (1883) specification "amphipneustisch oder mit Tracheenblasen oder Kiemen," no Chironomid larva has ever been found with functional spiracles. Minute non-functional spiracles occur on the abdomen of probably all Chironomid pupæ (Bause 1915, Potthast 1915, Rieth 1915), for it is by means of these that the tracheal exuviæ of the adult are withdrawn at emergence, but only in some Tanypinæ do they assume a condition which might possibly be functional (Thienemann and Zavrel, 1916), and even these are not to be compared with the well-developed spiracles of *Orphnephila.* Thienemann placed the group as the first subfamily of the Chironomidæ, with the Ceratopogoninæ second, chiefly on account of the abdominal armature and anal hooks of the pupa; he hoped that a comparison of the larval mouth-parts would confirm this relationship. There is, however, practically nothing in common between the two ; true, the labrum is elongated and flattened laterally as in Ceratopogonines, but it has no premandibles, structures which are pronounced throughout the Ceratopogoninæ (Goetghebuer, 1914) and Chironominæ*, and its dorsal, lateral, and ventral sclerites are peculiar to itself. The mandibles and maxillæ show no relation to one group more than another, and the narrow upturned labium is particularly distinctive. Ceratopogonines have a complicated chitinous hypopharynx within the head, which serves to grind up the food of those terrestrial forms living on solid matter (*Forcipomyia*, *Atrichopogon*) and possibly acts as a pump in those that take liquid food, while other Chironomids have a less involved but constant structure. *Orphnephila* has no such chitinous structure, but the fleshy hypopharynx and sickle-shaped pharyngeal lamellæ point to a relationship with Rhyphidæ, Ptychopteridæ, and, less closely, Culicidæ.

Other characters which set the genus apart are the saddle-like dorsal coverings of the larval body-segments, the antennæ, the protuberances of the head, the stout spl t macrochætæ of the head and body, and the larval method of progression. Add to this the inability of systematists to establish any relationship by means of the adult, and it will be obvious that the genus must revert to its original family status.

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* Tanypinæ have a pustule or fleshy lobe, which Thienemann and Zavrel homologise with the basal part of the premandibles.

I refrain from listing the larval and pupal family-characters, or suggesting the systematic position among the Nematocera, since the early stages of several new species have just been discovered in New Zealand and Tasmania by A. Tonnoir, and it is advisable to see first how they compare with ***O. testacea*.**

Summary.

Orphnephila has been placed by Kieffer and Thienemann as the first subfamily of Chironomidæ on the strength of the general appearance of the larva, the presence of pseudopods, the abdominal cuticular armature and anal hooks of the pupa, and the spiracular papillæ of the prothoracic horns.

Not one of these characters is peculiar to the Chironomidæ, while the following incontestably prohibit the inclusion of *Orphnephila* in that family:—

(1) The amphipneustic tracheal system of the larva.
(2) The peripneustic tracheal system of the pupa.
(3) The structure of the larval mouth-parts.

Further characters of less importance are the structure of the antennæ, the dorsal "saddles," the protuberances of the head, the split macrochætæ of the head and body, and the method of rapid progression.

Acknowledgements.

I desire to extend my grateful thanks to Dr. D. Keilin of the Molteno Institute for the loan of the preserved material sent him by Thienemann in 1914, and for his helpful suggestions and encouragement throughout the work. I am also indebted to Mr. F. W. Edwards of the British Museum for some larvæ, part of the same lot, given him by Dr. Keilin some years ago.

References.

Bause, E. (1913.) "Die Metamorphose der Gattung *Tanytarsus*." Arch. f. Hydrobiol. Supp. Bd. ii. 2, pp. 1–128.

Bezzi, M. (1913.) "Taumaleidi (Orphnetilidi) italiani." Boll. Lab. Zool. gen. agrar. Scuola Sup. Agricolt. Portici, vii. pp. 227–266.

Brauer, Fr. (1883.) "Die Zweiflüger des Kaiserlichen Museums zu Wien. III. Systematische Studien auf Grundlage der Dipteren-Larven, u.s.w." Denkschr. d. k. Akad. d. Wiss. Wien, xlvii.

Goetghebuer, M. (1914.) "Contributions à l'Etude des Chironomides de Belgique (Ceratopogoninæ)." Ann. de Biol. Lacustre, vii. pp. 165–229.

JOHANNSEN, O. A. (1903–5.) "Aquatic Nematocerous Diptera.—I. ('03) and II. ('05)." Bull. New York State Museum, lxviii. (Ent. 18 and 23).

KEILIN, D. (1912.) "Recherches sur les Diptères du Genre *Trichocera*." Bull. Sci. de France et Belg. 2, xlvi. pp. 172–190.

MALLOCH, J. R. (1915.) "The Chironomidæ, or Midges of Illinois, with particular reference to the Species occurring in the Illinois River." Bull. Ill. State Lab. of Nat. Hist. x. Article vi.

MEIJERE, DE, J. C. H. (1902.) "Ueber die Prothorakalstigmen der Dipterenpuppen." Zool. Jahrb. xv. Abth. f. Morph. pp. 623–692.

——. (1916.) "Beiträge zur Kenntnis der Dipteren-Larven und Puppen." Zool. Jahrb. xl. pp. 177–322.

POTTHAST, A. (1915.) "Ueber die Metamorphose der *Orthocladius*-Gruppe." Arch. f. Hydrobiol. Supp. Bd. ii. 2, pp. 243–376.

RIETH, J. TH. (1915.) "Die Metamorphose der Culicoidinen (Ceratopogoninen)." Arch. f. Hydrobiol. Supp. Bd. ii. pp. 377–442.

THIENEMANN, A. (1909.) "*Orphnephila testacea*, Macq., Ein Beitrag zur Kenntnis der Fauna Hygropetrica." Ann. de Biol. Lacustre, iv. pp. 1–35.

THIENEMANN, A., and ZAVREL, J. (1916.) "Die Metamorphose der Tanypinen." Arch. f. Hydrobiol. Supp. Bd. ii. 3, pp. 566–654.

EXPLANATION OF THE PLATES.

Key to Lettering.

ag.	Anal blood-gill.
ch.	Curved hairs.
cl.	Clypeus.
cp.	Conical processes.
ds.	Dorsal "saddle."
fc.	Felt chamber.
fh.	Fringe of hairs.
lp.	Lateral plate.
md.	Mandible.
mx.	Maxilla.
ph.	Prothoracic horn.
sl.	Sensory hairs of legs.
snp.	Sensory processes.
sp.	Spiracle.
spp.	Spiracular papillæ.
ss.	Striated setæ.
tr.	Trachea.
usp.	United posterior spiracles.
vp.	Ventral plate.

PLATE VII.

Fig. 1. Entire full-grown larva, lateral view. ×12.
Fig. 2. Prothoracic pseudopod. ×70.
Fig. 3. Pupa, dorsal view. ×12.
Fig. 4. One of the lateral thoracic groups of microchætæ, *sl* of fig. 1.
Fig. 5. Larval antenna.
Fig. 6. Distal end of prothoracic horn.
Fig. 7. Larval prothoracic spiracle.
Fig. 8. Pupal abdominal spiracle.
Fig. 9. Posterior spiracle, dorsal view.
Fig. 10. Extremity of larva, dorsal view.

PLATE VIII.

Fig. 11. Labrum of larva, dorsal view. ×200.
Fig. 12. The same, lateral view. ×200.
Fig. 13. Labium, ventral view.
Fig. 14. Left mandible and maxilla, inside view. ×200.
Fig. 15. The same, outside view. ×200.

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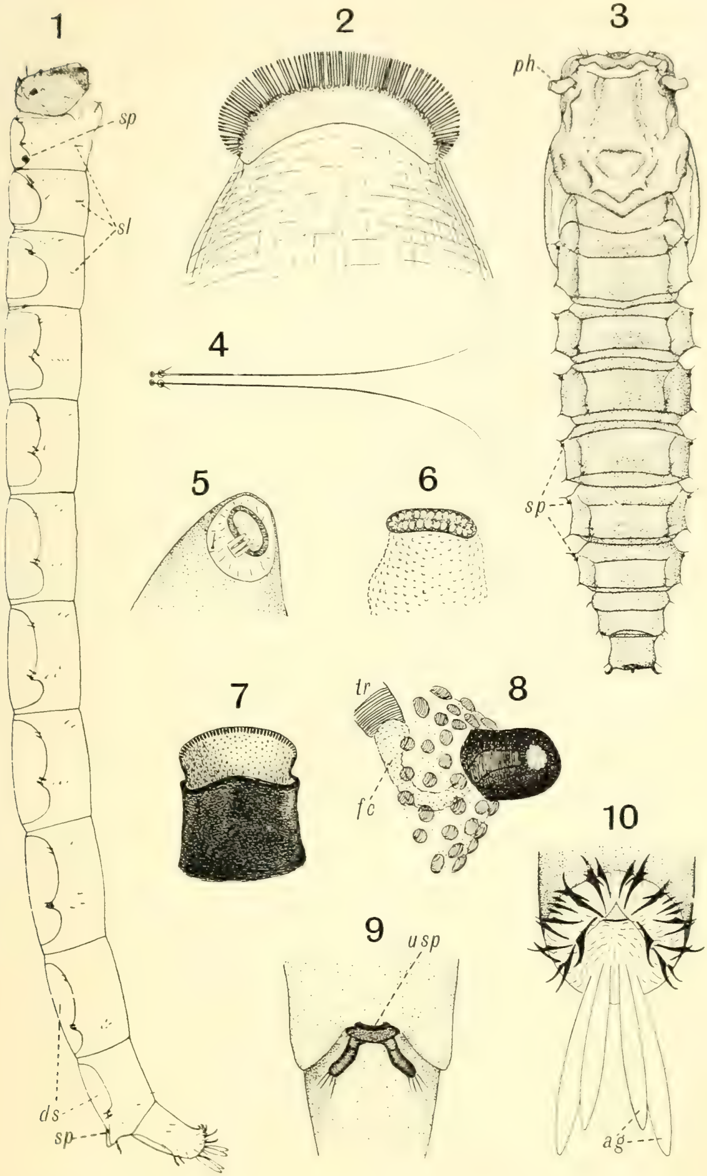

L. G. S. del.

Larva and Pupa of Orphnephila testacea, Macq.

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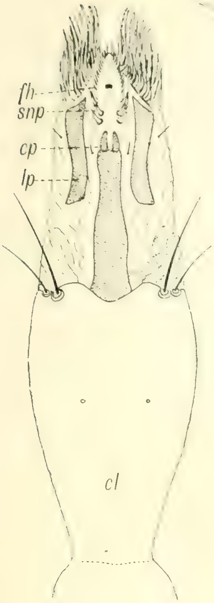

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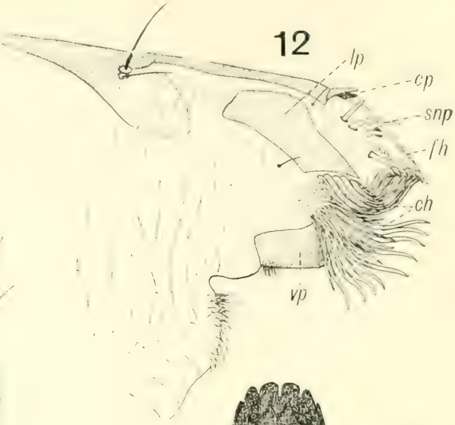

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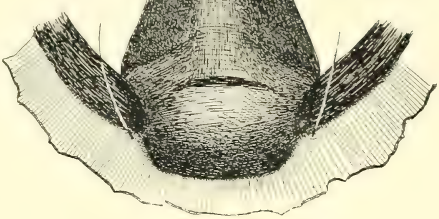

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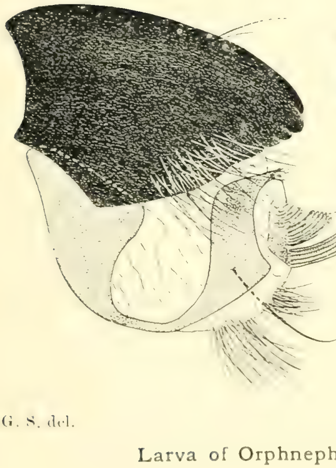

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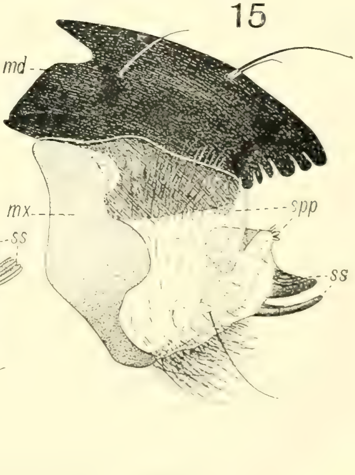

L. G. S. del.

Larva of Orphnephila testacea, Macq.